Vegetation maps based on remote sensing are informative predictors of habitat selection of grassland birds across a wetness gradient

Aurélien G. Besnard, Aurélie Davranche, Sébastien Maugenest, Jan-Bernard Bouzillé, Alain Vian, Jean Secondi

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Besnard, A.G. [1*], Davranche A.[2], Maugenest S. [1], Bouzillé J.B. [3], Vian A. [4], Secondi, J. [1]

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E-mail addresses:

aurelien.besnard@univ-angers.fr

aurelie.davranche@univ-angers.fr

sebastien.maugenest@univ-angers.fr

jan-bernard.bouzille@univ-rennes1.fr

alain.vian@univ-angers.fr

jean.secondi@univ-angers.fr

* *corresponding author*

[1] LUNAM University, University of Angers, GECCO (Group Ecology and Conservation of Vertebrates), 49045 Angers, France; Telephone number: 33 241 735 030

[2] LUNAM University, University of Angers, LETG - LEESA, 2 Boulevard Lavoisier, 49045 Angers, France

18 [3]UMR Ecobio Equipe Dynamique des communautés Campus de Beaulieu, 35042 Rennes,
19 France

20 [4] IRHS, 2 Boulevard Lavoisier - 49045 Angers, France

21

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23 Whinchat, Corncrake, Yellow Wagtail, Corn Bunting, Reed Bunting.

Abstract

Vegetation is a major environmental factor influencing habitat selection in bird species. High resolution mapping of vegetation cover is essential to model the distribution of populations and improve the management of breeding habitats. However, the task is challenging for grassland birds because microhabitat variations relevant at the territory scale cannot be measured continuously over large areas to delineate areas of higher suitability. Remote sensing may help to circumvent this problem. We addressed this issue by using SPOT 5 imagery and phytosociological data. We mapped grassland vegetation in a floodplain using two methods. We (i) mapped the continuous Ellenberg index of moisture and (ii) identified 5 vegetation classes distributed across the wetness gradient. These two methods produced consistent output maps, but they also provided complementary results. Ellenberg index is a valuable proxy for soil moisture while the class approach provided more information about vegetation structure, and possibly trophic resources. In spite of the apparent uniformity of meadows, our data show that birds do not settle randomly along the moisture and vegetation gradients. Overall birds tend to avoid the driest vegetation classes, i.e. the highest grounds. Thus, vegetation maps based on remote sensing could be valuable tools to study habitat selection and niche partition in grassland bird communities. It is also a valuable tool for conservation and habitat management.

Highlights

- We mapped grassland vegetation in a floodplain using two methods
- The Ellenberg index proves to be a valuable proxy for soil moisture
- Vegetation classes provided more information about vegetation structure

- Grassland birds do not settle randomly along the vegetation gradient
- Vegetation maps based on remote sensing are useful tools to study habitat selection

1. Introduction

Delimiting zones of protection is a major issue of conservation programs (McNeely, 1994; Moilanen et al., 2009). In order to identify core protection areas and optimize management, policy makers need robust background information like precise ecological requirements for target species. Grasslands present an interesting case in that respect because they often appear to human eyes as large expanses of uniform vegetation. For this reason, designing efficient protection areas in grasslands may seem challenging but this objective needs to be met. Due to anthropogenic changes, grassland birds are threatened in several part of the World (Azpiroz et al., 2012; Brennan and Kuvlesky, 2005; Tryjanowski et al., 2011; Tucker et al., 1994). Agri-Environmental Schemes (AES) were implemented in the 1990's within the European Union to subsidize grassland management compatible with breeding but many species have continued to decline (Kleijn et al., 2006). Precise knowledge of habitat selection for target species is therefore crucial to design new and more ecologically oriented AES measures in areas where conservation objectives partly failed.

Although their breeding habitat may seem homogeneous, grassland species do not settle at random in meadows. Spatial variations in density are frequently observed. For instance, many species are area-sensitive and avoid small fragments of habitats (Besnard and Secondi, 2014; Davis and Brittingham, 2004; Helzer and Jelinski, 1999). Even in larger patches, they tend to avoid landscape features like hedges because of higher predation risk (Morris and Gilroy, 2008). Vegetation itself offers various level of suitability for nesting. Vegetation structure is a major feature that influences the settlement of grassland birds (Fisher and Davis, 2010; Jacobs et al., 2012). Plant community largely determines arthropod assemblages (Schaffers et al., 2008) and therefore the quantity and quality of available trophic resources (Britschgi et al., 2006). Grassland birds tend to

prefer areas with higher densities of flowers during the breeding season (Fischer et al., 2012). This preference may reflect higher prey availability to feed the young (Oppermann, 1990). Vegetation cover also determines predation risk (Ejsmond, 2008), particularly the ability of birds to hide their nests under the canopy (Whittingam and Evans, 2004). Therefore, grassland birds tend to select nest site with taller swards and denser vegetation (Davis, 2005). In addition, some species need herbaceous perches for foraging and territorial defence (Fischer et al., 2012; Oppermann, 1990).

Soil moisture is a major factor of grassland ecology (Price, 2002; Suzuki et al., 2006). It is considered as the main driver of vegetation patterns in most regions (Moeslund et al., 2013),. Flood is a recurrent phenomenon that generates a wetness gradient and structures vegetation communities (Martinez and Letoan, 2007). However, wetness is also influenced by local environmental conditions like altitude, microtopography, or soil. Fortunately, vegetation has the property to integrate all the components of wetness (Goward et al., 1991). Mapping vegetation in relation to its affinity for moisture is expected to provide informative predictors to analyse habitat selection in grassland birds and improve the management of these habitats. Satellite remote sensing techniques are promising tools in this regard. They provide vegetation data with a spatial resolution high enough to analyse habitat selection in birds across ecological gradients. Furthermore, satellite images often cover geographical ranges large enough to delineate areas with different levels of conservation priority (Guo, 2004; Poulin et al., 2010).

We assessed two methodological approaches to describe the variation of grassland vegetation across the wetness gradient in floodplains. We used the Ellenberg moisture index that attributes a value to each vegetal species, corresponding to its affinity for soil moisture (Ellenberg et al., 1992). We computed a continuous wetness gradient based on the mean Ellenberg index of the local vegetation community to map the wetness gradient across a floodplain. In addition, we tested a

discrete method to map vegetation classes as defined by the phytosociological approach (Tichý, 2002). A vegetation class is “a system of vegetal organisms with a floristic composition that is statistically repetitive” (Biondi, 2011). Each class may offer a specific level of suitability for birds depending on its physical properties and the various resources it provides. In grasslands, these vegetation classes may therefore be an informative proxy to describe habitat requirements of bird species. This approach may be easier to apply for managers since habitats are determined and their conservation prioritized according to vegetation associations, for instance in the European Union (Davies et al., 2004). Finally, AES are implemented in our study area to protect grassland and birds. We tested if AES types were related to vegetation community, i.e. the hydrological functioning of the floodplain, and if the spatial distribution of AES matched habitat selection of birds as described by vegetation.

105

106 ## 2. Methods

107 *2.1 Study area*

108 The study area covers the floodplains of the Loire River and its main tributaries around Angers
109 city in France (47.48, -0.56) (Fig. 1). Hydrological flow is relatively undisturbed by anthropogenic
110 developments in contrast to other floodplains of similar size in Western Europe (Hesselink et al.,
111 2003). Due to frequent floods, extensively managed grasslands still represent the main land cover
112 type. Agricultural practices consist in mowing meadows once a year in June-July and in allowing low
113 intensity grazing by cattle during vegetation regrowth. Considering the shallow slope of the ground,
114 plant community mainly depends on soil wetness and submersibility. Owing to their management,
115 these grasslands still host several patrimonial bird species, like the Corncrake (*Crex crex*), known to
116 be highly sensitive to intensive agriculture (Green et al., 1997a). Many grassland bird species
117 collapsed in the second part of 20th century, mainly due to the intensification of practices (more
118 efficient machinery, fertilisation, advanced mowing schedule). Agri-environmental schemes (AES)
119 that were implemented locally mainly consisted in delaying hay mowing. The proportion of grassland
120 under AES is quite high in the study area (45% in 2011). Several levels of AES measures are present in
121 the study area, differing mainly by the earliest mowing date. For clarity, we aggregated parcels in two
122 sets: those mown in June (3 540 ha) and those mown in July (1 571 ha). Mowing before July causes
123 high mortality in broods (Broyer, 2007; Green et al., 1997b). Therefore, we considered that meadows
124 mown in June were not suitable for the sustainable breeding of grassland birds.

125

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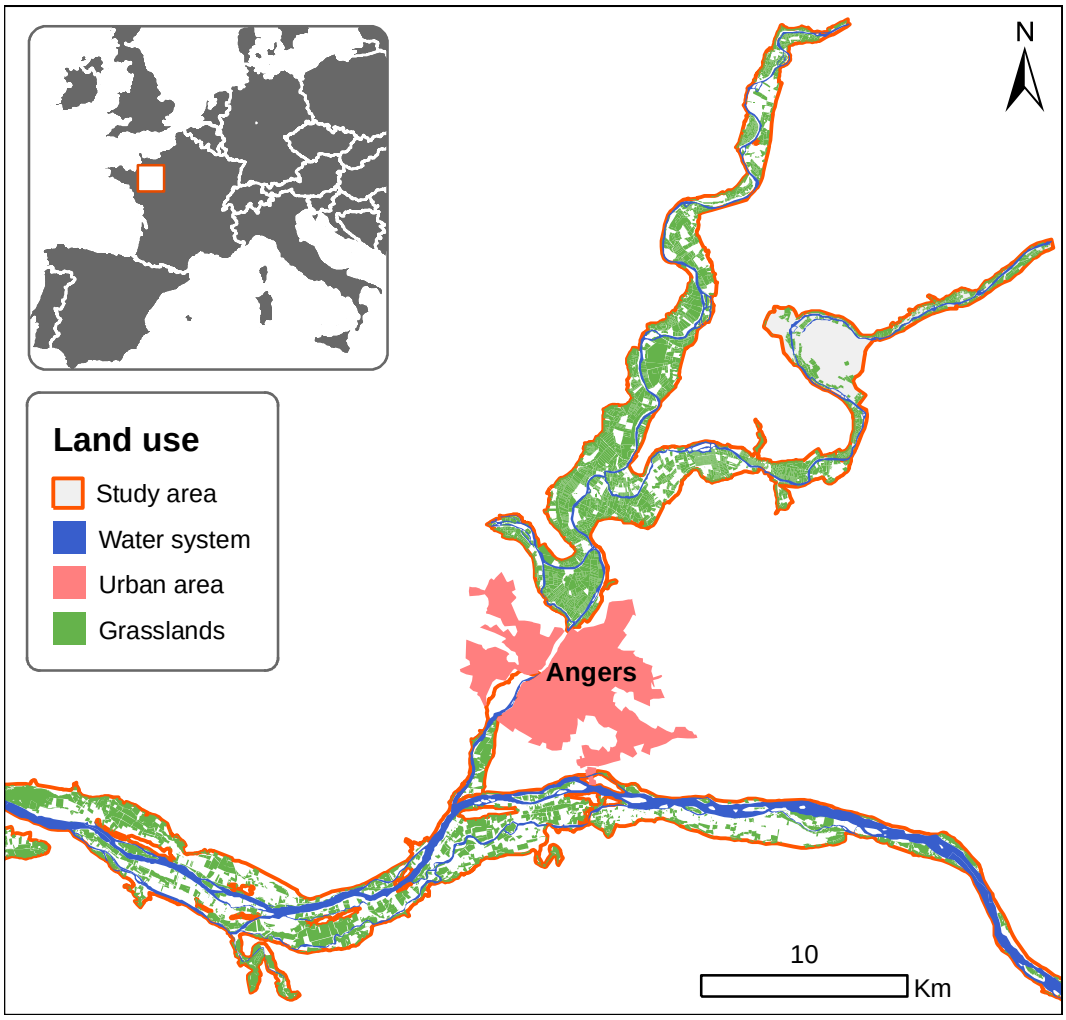
Figure 1: Map of grassland distribution in the study area. The inset shows the location in Europe.



2.2 Vegetation relevés and phytosociological classification

We conducted phytosociological relevés on 107 plots to describe vegetation community across the whole study area. Survey was carried out from May 16th to June 10th 2011 to ensure the reliable identification of plant species. A plot was defined by the standard 16m² quadrat method (Chytrý and Otýpková, 2003). Quadrats were selected in a larger zone of homogeneous vegetation to limit the environmental effects of other land cover bordering the pixel of the relevé during the remote sensing

process. We sampled as many contrasting situations along the flooding gradient as possible basing on our knowledge of the study area. Sampling plots were positioned using a Differential Global Positioning System (DGPS), through a Trimble© Juno© SB. The estimated georeferencing error after post-processing was 6 m maximum. However it was lower than 4m for 93% of plots. All species in the quadrat were identified using either a local specific flora (Corillon, 1981) or a vegetative flora (Eggenberg and Möhl, 2013) when necessary. Area covered by each species was evaluated using a Braun-Blanquet coefficient (Braun-Blanquet, 1964). We then classified relevés with JUICE software (Tichý, 2002), using the TWINSPAN method (Hill, 1979), including standard relevés from a previous study conducted in the same area (Foucault, 1984) as referentials for the classification. This method classifies relevés according to their similarity in order to identify phytosociological taxa. We identified five taxa along the wetness gradient in the area: 1. Phalaridion arundinaceae, Kopecky 1961; 2. Gratiolo officinalis-Oenanthetum fistulosae inferior, De Foucault, 1984 nom. Ined; 3. Gratiolo officinalis-Oenanthetum fistulosae superior, De Foucault 1984 nom. Ined; 4. Senecio aquatici-Oenanthetum mediae, Bournerias et al. 1978; 5. Arrhenaterion elatioris, Hoch, 1926. The wettest and the driest have been considered at the alliance level owing to the diversity of associations encountered in the field for these two taxa. The three intermediate classes (2-4) have been specified to the association level because their observed compositions matched the original descriptions. However, the Gratiolo officinalis-Oenanthetum fistulosae was split in two due to the wide area it covered and named in accordance with the type relevés described by De Foucault (1984). We tested the significance of those partitions with a non-parametric multivariate analysis of variance (Anderson, 2001) using *adonis* from the *vegan* R-package (Oksanen, 2013).

2.3 Wetness Ellenberg index

159 In order to quantify the wetness gradient, we used the wetness Ellenberg index. Ellenberg
160 indexes determine the affinity of each species for environmental parameters like light, temperature,
161 or nitrogen in soil (Ellenberg et al., 1992). We used here moisture affinity scores which are available
162 for each species (Hill et al., 1999). A value of 1 is given to a specialist of the driest habitats and a
163 value of 12 for a specialist of the wettest habitats. The indicator value of Ellenberg scores has been
164 evaluated by a field study that concluded that they were very good descriptors of the local
165 environment (Schaffers and Sýkora, 2000). For each plot, we averaged Ellenberg values of all species,
166 regardless of their cover, to obtain a single value. We considered this value as a proxy of soil wetness
167 at the plot scale. We computed average Ellenberg scores weighted by species cover and unweighted.
168 The unweighted method gave more realistic outputs. This is because cover depends mainly on the
169 sociability, for example the cover of grasses species is often high whereas sparse species like
170 *Fritillaria meleagris* can have a more informative value In addition, weighted average penalize rare
171 species that often display narrow niches and are informative indicators.

172

173 *2.4 Mapping*

174 A SPOT 5© satellite image 2.5m colour, correction level 2B (allocation accuracy less than 10m),
175 was acquired on May 5th 2011. These scenes are provided with three bands: B1 (green: 0.50 to 0.59
176 µm), B2 (red: 0.61 to 0.68 µm), B3 (near-infrared NIR: 0.79 to 0.89 µm). A mask of all the meadows
177 within the floodplains was applied on this scene (60 km long x 60 km wide) to delineate the whole
178 study area using in ARCGIS version 10 (Environmental Systems Research Institute, Meudon France).
179 All analyses were conducted with this mask. Conditions of image acquisition were optimal with a low
180 incidence angle (4.77°) and cloud cover less than 10%. Spring 2011 was relatively dry so all the study
181 area was emerged but a small 41-ha zone that is kept flooded to provide spawning sites for fishes. A

vector layer of vegetation plots (quadrats) was created using their GPS coordinates. Circular buffers (diameter 4 m) centred on each point were drawn to get a vector layer of polygons of the vegetation plots. Then, we used the Spatial Analyst module to extract the mean radiance values of every sampling plot for each spectral band. We then calculated for each plot multispectral indices (Table 1) adapted for SPOT bands (see the method from Davranche *et al*. (2010 and 2013)).

Table 1 Multispectral indices used in this study.

ID index	Multispectral index	References
1	Differential Vegetation Index (DVI)	Richardson & Everitt, 1992
2	Index of free water (IFW)	Adell & Puech, 2003
3	Normalized Difference Vegetation Index (NDVI)	Rouse *et al*., 1973
4	Normalized difference water index (NDWI)	Mc Feeters, 1996
5	Optimized Soil Adjusted Vegetation Index (OSAVI)	Rondeaux *et al.*, 1996
6	B3	Spot image
7	B2	Spot image
8	B2/B1	This study
9	Soil Adjusted Vegetation Index (SAVI)	Huete, 1988
10	Brightness index (BI)	Kauth and Thomas, 1976
11	Simple ratio (SR)	Pearson & Miller, 1972
12	B1	Spot image
13	B1-B2	This study
14	(B1-B2)/(B1+B2)	This study
15	$B1^2/B2$	This study
16	Vegetation indice (VI)	Lillesand & Kiefer, 1987
17	Water index (WI)	Davranche et al, 2013
18	Water impoundment index (WII)	Caillaud *et al.*, 1987

191 Classification of the 5 vegetation classes was performed using a decision tree with a dichotomous
192 partitioning (Breiman et al., 1984). It was performed for each class using a binary coding: presence or
193 absence. We also tested a multiple-class classification, where we attempted to identify all classes in
194 the same analysis, but this method gave poor results. The Rpart package (Recursive PARTitioning,
195 Therneau and Atkinson, 1997) in the R software version 2.15.2 software (Rdevelopment core team,
196 2012) was used. This method is based on the cost complexity parameter (cp) for pruning. As
197 described in Davranche et al. (2010) for unbalanced samples, we used the cross-validation procedure
198 called CV-1SE (Esposito et al., 1999) for pruning with 10 subsets and iterative runs of the algorithm
199 (Breiman et al., 1984) to select the cp and the prior parameter. Cross-validation is well suited to small
200 samples (Breiman et al., 1984)., so it can be recommended when no additional independent sample
201 is available.

202 The distribution of wetness Ellenberg index was checked for normality. We used linear models to
203 test whether index values obtained from field relevés could be predicted from remote sensing
204 variables). Models with all combinations of predictors were computed with the 'lm' function from
205 the R-package 'stats'. Model selection was carried out using the 'dredge' function of the R-package
206 'MuMIn' (Barton, 2013). The best model was selected according to the lowest AICc value (Burnham
207 and Anderson, 2002) (Appendix 1 in Supplementary material). As advised by Symonds and Moussali
208 (2011), we assessed the goodness-of-fit of this best AICc model, by calculating the coefficient of
209 determination (R^2) and the normalized root-mean-square error (NRMSE) between the predicted and
210 observed values.

211

212 *2.5 Bird census*

213 The study area host several breeding grassland species, some of which have been declining for
214 several decades in Western Europe (Tucker et al., 1994). We sampled the 4 dominant passerine
215 species in this small avian community: the Whinchat *Saxicola rubetra*, the Yellow Wagtail *Motacilla*
216 *flava*, the Corn Bunting *Emberiza calandra* and the Reed Bunting *Emberiza schoeniclus* (Noël, 2003).
217 We scanned every hay meadows of the study area during the 2011 breeding season to locate birds.
218 We used binoculars (10x42) and a spotting scope (20x-60x, 66mm) to detect and identify species.
219 Fieldwork was performed from April 13th to June 17th 2011 in good weather conditions (no
220 precipitation and low wind) to optimize bird detection and avoid the recording of migrating birds.
221 The time of day was not considered to maximize the area surveyed during the breeding season.
222 However, the detection rate of these species remains relatively high throughout the day, even in the
223 late afternoon when males rest on the top of vegetation. All occurrences were located on a map
224 (IGN© 1:25 000), and reported on a GIS software (ArcGIS© 10) by the same observer. We also used
225 the Corncrake database from LPO France (French official BirdLife partner). These data were collected
226 in 2011 by volunteer ornithologists who located singing males at night. Like for passerines, Corncrake
227 data were compiled in a GIS dataset. Overall, we observed 451 Whinchats, 151 Yellow Wagtails, 114
228 Corn Buntings, 174 Reed Buntings, and we used 479 occurrences of Corncrake across the study area.

229

230 2.6 Statistical analyses

231 In order to compare Ellenberg index values on bird locations with background values, we defined
232 1 501 background plots distributed across a 250m-grid. We created a buffer zone of 100m around
233 each bird location and background plot. We extracted the average wetness index for all pixels
234 included in the buffer area. For each bird species, we then compared mean wetness values on
235 location buffers and background plots using a Wilcoxon test based on bootstrap (1000 iterations of

236 background values with n≥114 corresponding to the sample size of each species) with the R software
237 (version 3.0.2).

238 Similarly, we extracted the mean area covered by each vegetation class within 100m-buffers
239 around each bird location. Knowing that each class was calculated independently, a pixel can be
240 assigned to several classes. We compared values for each class to the area covered by the same class
241 in the whole study area, and tested the differences between the two variables using a Wilcoxon test.
242 We measured selection or avoidance by birds for each class by calculating the difference in the
243 distributions of vegetation classes between bird and random location using background plots
244 described above (n=1 501).

245 In order to compare the two methods (Ellenberg wetness index and vegetation classes), we used
246 44 transects of 500m long surrounded with a 100m-buffer (i.e. 13.1 ha). These transects were
247 distributed across the floodplain in open meadows selected for their suitable landscape for grassland
248 birds. These were previously used with success to investigate the interest of the topographic
249 wetness index as a predictor of grassland bird distribution (Besnard et al., 2013). For the two
250 vegetation maps, we extracted mean values (Ellenberg index and vegetation class) on these transects
251 and we fitted a linear model between these two datasets. We also used Chi-squared tests to test
252 whether vegetation classes and bird distributions were randomly distributed across mowing dates.
253 All tests were carried out using R software (version 3.0.2). Finally, we could determine the pattern of
254 flooding susceptibility in 35 plots spread across the study area during a spring flood (April-June) in
255 2013. We sampled these plots twice a week before, during and after the flood, and derived a flood
256 index which corresponds to the number of times the plots were flooded. To determine whether
257 Ellenberg index was related to submersibility, we fitted a linear model between flood index and
258 mean Ellenberg index on plots.

3. Results

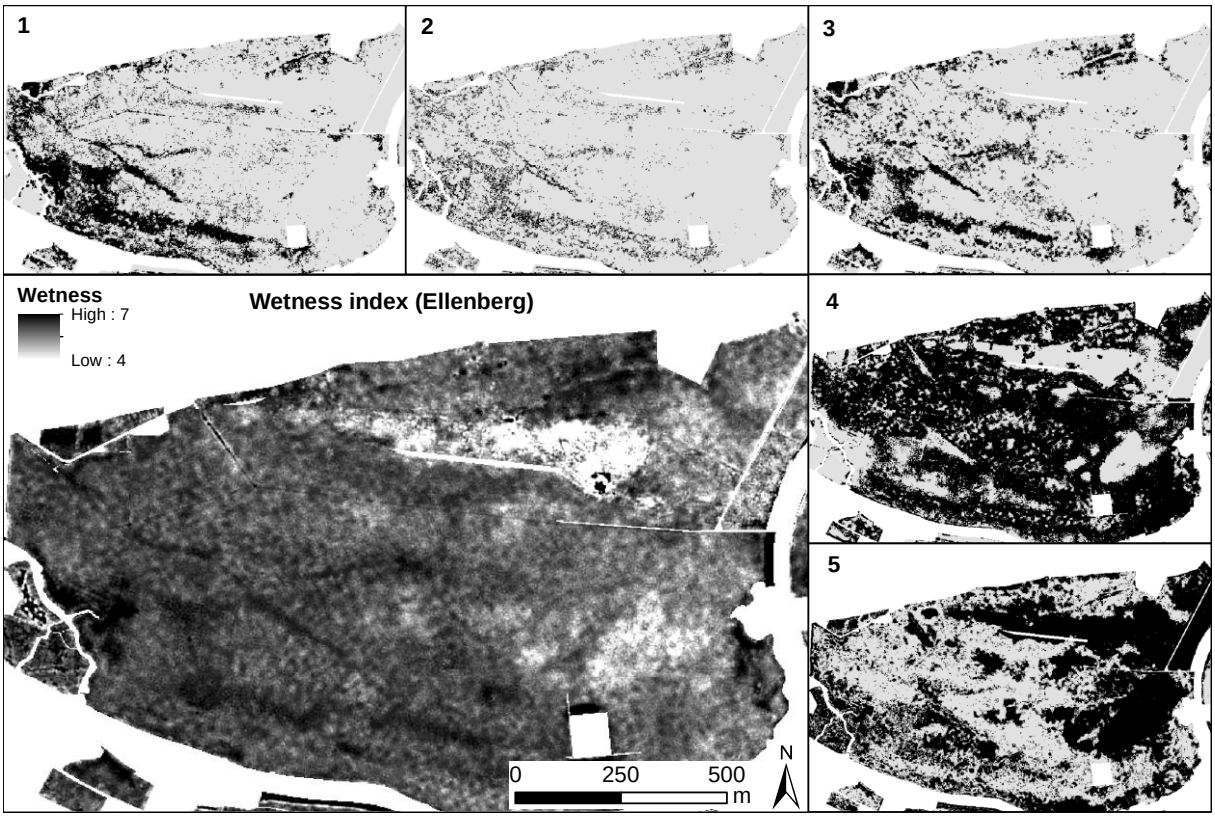
Using remote sensing method we could map the wetness gradient based on Ellenberg moisture index across the hay meadows of the study area (Fig. 2; Best model : df = 7, LogLik= 110.97, AICc= 237.08, weight = 0,00048, R^2 = 0.41, NRMSE = 19%; Y= 114,10 + 0,19*DVI + 49,73*NDWI + 1,65*B2 + 164,96*B2/B1 + 0,65*$B1^2$/B2 (More details on model selection in Table S2 in Supplementary material). The map was consistent with the observed flood susceptibility pattern ($F_{1,33}$ =25.09; p<0.001, adjusted R^2 = 0.43) (Fig. 3a). The resulting trees for the classification of vegetation classes provided the following error rates C_1: 9%, C_2: 14%, C_3: 16%, C_4: 16%, C_5: 10%. Plant species composition was significantly different between classes as defined by Twinspan ($F_{1,106}$ = 5.62 ; p=0.001). Using transect data, we found that average vegetation class was strongly correlated with Ellenberg moisture index ($F_{1,42}$ = 116.1; p<0.001; adjusted R^2 = 0.73) (Fig. 3b) confirming the value of these two methods to map wetness gradients. We noticed that the cover of class 5 is probably overestimated on a part of the wettest area. This area was submerged by water several weeks before the image capture and vegetation reflectance was modified by alluvium deposits. It was classified as belonging both to the wettest classes (1-3) and class 5 but field data confirm that this latter class was not observed there. This classification error causes an underestimation of avoidance of class 5 by birds because this area exhibit high bird densities. Nevertheless, we detected an avoidance of this class for 4 species. Thus, this limit does not alter the conclusion of this study.

All bird species except the Corn bunting settled in meadows with Ellenberg values higher than random locations in the study area (Bootstrap based on Wilcoxon test; p<0.001) (Fig. 4 and Table 2). Yet, this species also tended to select plots with high Ellenberg values (p=0.10 ± 0.16). Generally, birds selected wetter hay meadows than available in the study area (Fig. 4 and Table 2). The analysis

of vegetation classes provided supplementary information (Fig. 5). Except for the Corn Bunting, the three wettest vegetation classes represented a larger proportion of the buffers around bird locations than available (Table 3). For all species but the Whinchat, the driest vegetal class (5) represented a smaller proportion of the buffer area around bird locations than expected by chance. For all species, vegetation class 3 was more represented around bird location than available. Results were more contrasting for vegetation class 4. It was more represented around bird locations for the Corn Bunting and the Whinchat, whereas it was less represented for the Reed Bunting and the Corncrake. More globally, the pattern of habitat selection for vegetation classes was different between species

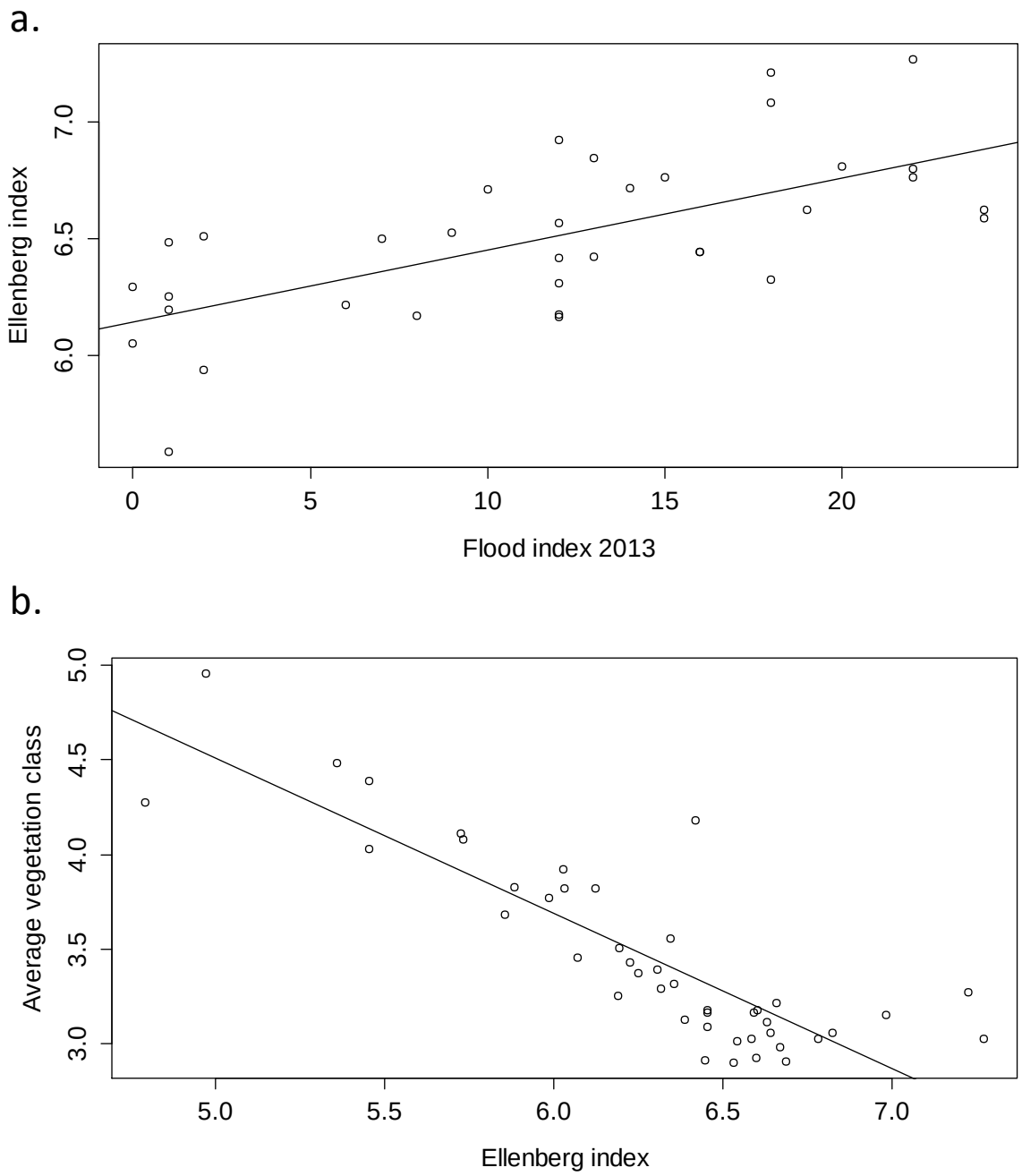
The proportion of area covered by each vegetation class differed between AES contract types ($Chi^2 = 350.75$, df = 4, $p<0.001$) (Fig.5). The driest vegetal classes (5) covered a larger proportion of the meadows available for mowing in June (47 %) than in July (23%). Logically, we observed the reverse pattern for the wettest vegetal classes 1, 2 and 3 which represented a lower proportion of the meadows mown in June (31%) than in July (55%). The proportion of the area covered by vegetation class 4 was constant between both periods (22 %). Regarding mowing date, birds of all species settled more frequently in parcels available for mowing in July than expected by chance ($Chi^2 = 521.10$, df=4, $p<0.001$). In the study area only 22 % of meadow area was mown in July whereas between 45 % and 66 % of birds settled in this parcels (Fig.5).

Figure 2: Maps extract of the study area representing with the wetness gradient as determined by Ellenberg moisture index and vegetation classes (1 the wettest and 5 the driest). Grassland areas were used as a mask prior to mapping.



304

305 **Figure 3: a.** Linear relationship between Ellenberg moisture index and flood susceptibility index
306 as measured on 35 plots during a flood event in 2013. **b.** Linear relationship between
307 Ellenberg moisture index and average vegetation class (1 is the driest, 5 the wettest class) in hay
308 meadows (n=44).



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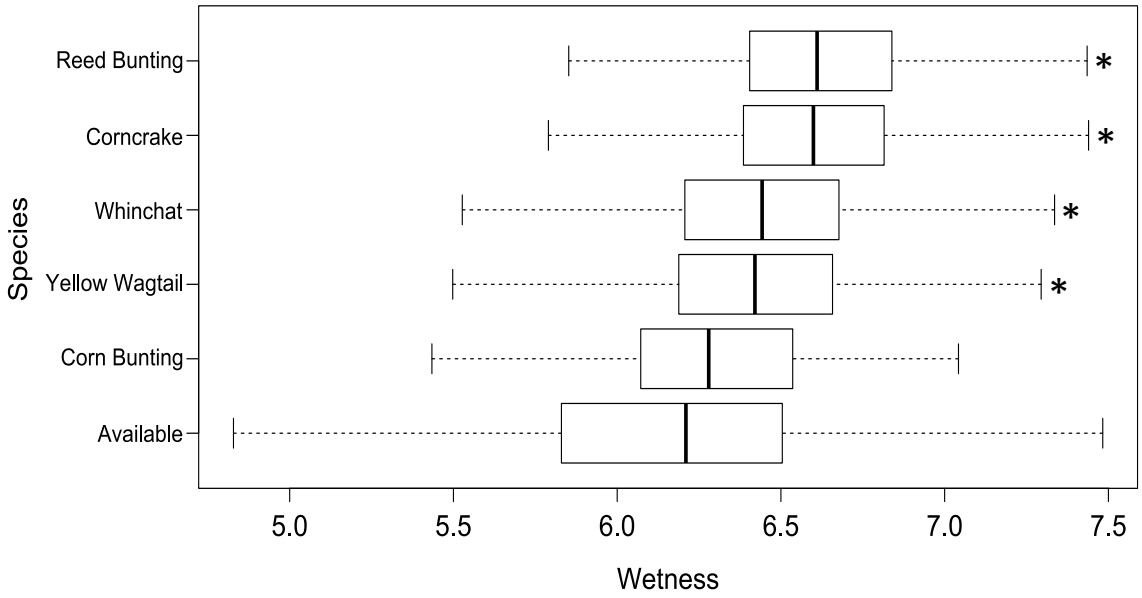
310 **Figure 4:** Boxplots of distribution of Ellenberg moisture index calculated for 100m buffers around
311 species occurrences and in the study area (available). * indicates that a species did not settle at
312 random across the wetness gradient and significantly preferred wetter meadows (Wilcoxon signed-
313 rank test).


Reed Bunting
Corncrake
Whinchat
Yellow Wagtail
Corn Bunting
Available
Species
5.0
5.5
6.0
6.5
7.0
7.5
Wetness

314

315

316

Figure 5: Distribution of bird occurrences across vegetation classes in floodplain grasslands. The first histogram represents the proportion of each class in the study area. All other histograms represent the differences between the proportion of each vegetation class available in the study area and the proportion of these classes in a 100m-buffer around bird occurrences. Filled symbols indicate whether birds significantly selected or avoided this class (Wilcoxon signed-rank tests). Open symbols indicate that no selection or avoidance was detected (see values in Table 2). Vegetation classes were ranked from the wettest (1) to the driest (5).

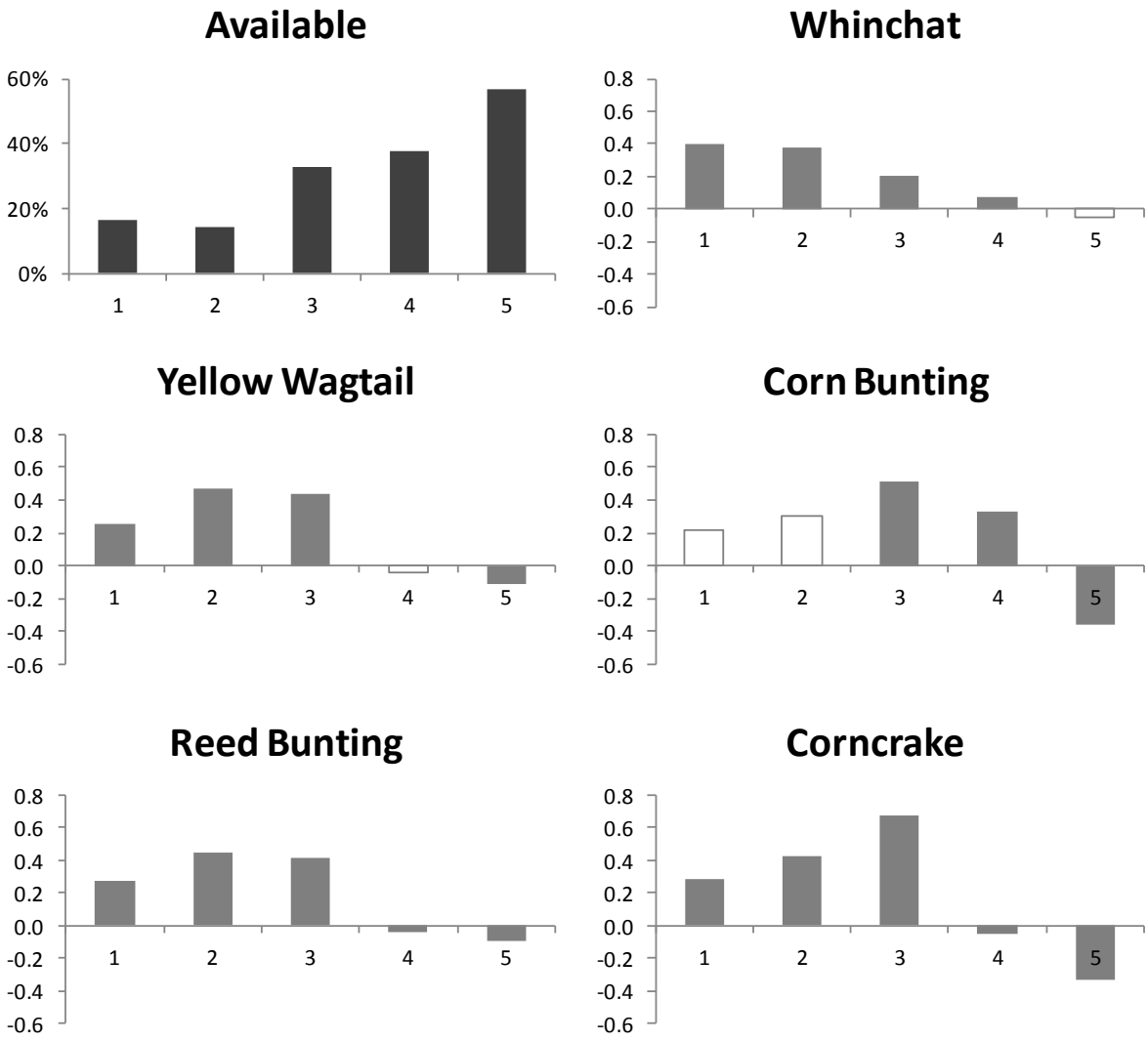


Figure 6: (left panel) Comparison between the distribution of the five vegetation classes (from C_1 the wettest to C_5 the driest) observed across the grasslands of the study area and in the parcels under AES contracts. Mowing dates were allowed either in June or in July. (right panel) Comparison between the proportion of area available for mowing in June and July, and the proportion of the population for each bird species on these two management options.

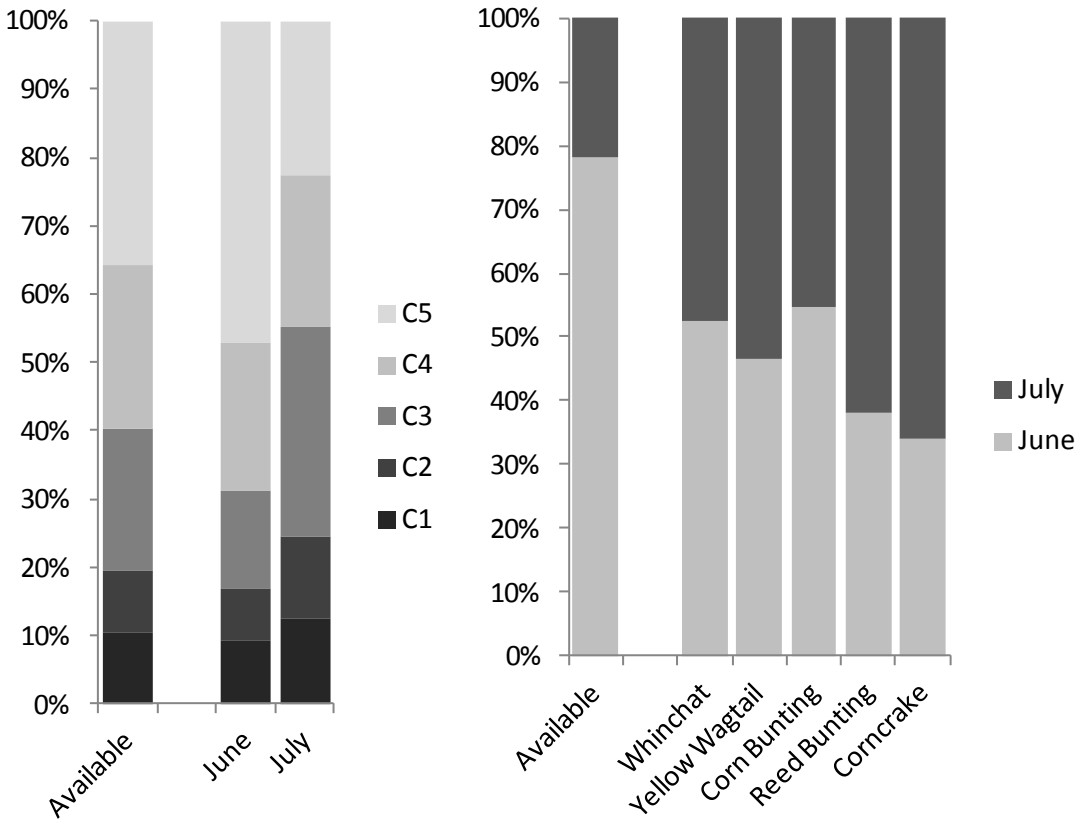


Table 2: Test of habitat selection comparing Ellenberg index in 100m buffers around bird occurrences and random background locations, and using bootstrap results of Wilcoxon tests. Selection is considered to occur when p-value < 0.05, in this case the value is in bold.

	p average	2.50%	97.50%
Yellow Wagtail	**<0.001**	<0.001	<0.01
Corn Bunting	0.10	<0.001	0.62
Reed Bunting	**<0.001**	<0.001	<0.001
Corncrake	**<0.001**	<0.001	<0.001
Whinchat	**<0.001**	<0.001	<0.001

Table 2: Cover of each vegetation class within a 100m buffer around species occurrences and random background locations. A species is considered to settle more often than by chance in a given class when p-value < 0.05 (value in bold). Vegetation classes were classified for the wettest (1) to the driest (5). V is the Wilcoxon statistic and p is the corresponding p-value.

	1		2		3		4		5	
	V	p	V	p	V	p	V	P	V	p
Whinchat	62531	**p <0.001**	72221	**p <0.001**	66832	**p <0.001**	57279	**p <0.05**	46081	0.078
Yellow Wagtail	6593	0.112	8265	**p <0.001**	9339	**p <0.001**	5082	0.223	3786	**p <0.001**
Corn Bunting	3279	0.998	3615	0.341	4744	**p <0.001**	4404	**p <0.01**	1297	**p <0.001**
Reed Bunting	10291	**p <0.001**	13992	**p <0.001**	14941	**p <0.001**	6178	**p <0.05**	3609	**p <0.001**
Corncrake	68357	**p <0.001**	94337	**p <0.001**	108846	**p <0.001**	47725	**p <0.01**	10081	**p <0.001**

4. Discussion

Floodplain grasslands, the location the work was conducted, do not represent a uniform habitat. Soil moisture gradient generates spatial variation in the composition of plant community (Fig. 2). Using remote sensing, we characterized Ellenberg index at the pixel scale (2.5 m) so that we could map the moisture gradient at a high spatial resolution. The ability of this index to represent wetness was confirmed by the positive relationship with flooding susceptibility, a variable that we could extract from direct observations in the field during a flood event (Fig 3a.). The vegetation community showed some discontinuity across the soil moisture gradient though using the TWINSPAN method (Hill, 1979) we could define five phytosociological classes spread across the soil moisture range. Average level of association in a plot was strongly related to Ellenberg wetness index (Fig 3b.). These remote sensing data provided us with a layer of an informative predictor, the moisture gradient, to analyse fine habitat selection of birds.

Basing on these data, we found that no bird species settled randomly across the grasslands of the study area. They rather selected parcels depending on vegetation composition, which itself reflected the moisture gradient. The wettest meadows (high values of Ellenberg index) hosted generally more grassland birds in 2011 (Fig. 4), a distribution pattern observed in other years (Noël, 2003, A. Besnard unpublished data). Even the Corn Bunting, which exploits a large range of open habitats (Donald and Evans, 1995) showed a tendency to select the wettest meadows. Consistently, birds did not settle randomly according to vegetation class. This approach provided additional information to the wetness index. The Reed Bunting and the Corncrake, specialists of grasslands and wetlands with tall sward (Brickle and Peach, 2004; Green et al., 1997a), settled in areas containing a higher proportion of the wettest vegetation classes (1-3) than available across the floodplain (Fig. 3b). They also avoided plots with a high proportion of the driest classes (4-5). Similarly, the Whinchat which is a

specialist of extensively managed hay meadows (Müller et al., 2005), and the Yellow Wagtail which can breed in alternative habitats like crops (Gilroy et al., 2011) preferentially selected the wettest meadows. Finally, the Corn Bunting selected grasslands with a higher proportion of classes 3 and 4, and avoided both wettest and driest classes. Overall, no species selected areas covered by a large proportion of the driest class (5), confirming the results obtained by the method based on Ellenberg index. Interestingly, this latter class is the most represented in the study area (36%) whereas classes 1, 2 and 3 cover respectively only 10%, 9% and 21%. Species' responses to class 4 were more diverse. The Corn Bunting settled in areas offering a large cover of this class, and the Whinchat tended to slightly show the same pattern. In contrast, the Reed Bunting and the Corncrake tended to avoid areas where this type of vegetation was more abundant than observed in average in the study area. These results highlight interspecific differences in habitat selection and are consistent with the ecology of these birds. Yet, differences were usually described for a larger range of ecological conditions (Jacobs et al., 2012). It is thus particularly interesting to observe that it is possible to determine species-specific habitat selection profiles within a much narrower ecological range. Furthermore, species tended to keep their relative position in the wetness gradient with the restricted ecological range of conditions encountered within the grasslands of these floodplains.

Our results suggest that the wettest grasslands (high Ellenberg index and large proportion of classes 1-3) were the most suitable for birds. Intermediate class (4) were suitable for some species and avoided by others but selection or avoidance was lower. In contrast, the driest grasslands (class 5) tended to be avoided by all species. We can draw hypotheses to explain this pattern. The wettest classes can be characterized by a higher forb cover than drier class. We expect trophic resources (e.g. pollinator insects) (Oppermann, 1990; Pywell et al., 2011) and vegetation structure to depend on the grass/forbs ratio (Oppermann, 1990). All bird species are mainly insectivorous during the breeding season (Brickle, 1999; Brickle and Peach, 2004; Britschgi et al., 2006; Davies, 1977; Green et al.,

1997a). Therefore, the quantity or quality of trophic resources may be higher on the wet end of the moisture gradient than on its dry end. Vegetation structure may be of importance too as a higher proportion of forbs may provide better sites for building nest and more perches for foraging and social activities as well as reducing predation risk.

Flood, meadow management and bird conservation

Vegetation mapping based on remote sensing technique appears as a helpful tool to investigate habitat selection in grassland habitats and to guide conservation actions. In our study area, the proportion of any given vegetation class drastically differed between AES contract types (Fig. 5). Early mown parcels (June) were mostly covered by the driest vegetal classes whereas parcels mown later (July) were mostly covered by the wettest classes. This is a logical outcome of a scheme based on volunteering. Farmers tend to select the contract level which minimizes the loss of hay quality. On the driest meadows, that are mature early, farmers preferentially choose contracts with early mowing dates. It results that the spatial pattern of mowing dates matches fairly well the wetness gradient across the study area.

It is possible to describe the wetness gradient of an area using only topographical data (Besnard et al., 2013; Beven and Kirkby, 1979). However, the low altitudinal variation in floodplains may not be grasped by the resolution of available many digital elevation models, that are the raw data for computing topographic methods, which limit our ability to map accurately the wetness gradient. Also pixel size of these models may not be appropriate or relevant in species with small territories for which small-scale features of the habitat may matter, for their nest site for instance. In contrast, the high resolution provided by satellite imagery (2.5 m here) allows adjusting the spatial scale of the analysis to the scale relevant for any bird species. Digital elevation models can be available with very

high altitudinal resolution in some areas, in which case it could be interesting to carry out a comparative assessment of these two methods. However, it is important to outline that unlike topographical methods the local plant community is an integrative measure of various processes generating soil moisture (topography, soil composition and climate). Vegetation mapping takes also into account anthropogenic modifications (like dams or drainages) which cannot be integrated by topographic methods, for instance in cultivated lands where vegetation depends mainly on agricultural processes. Finally, the remote sensing method is more ecologically realistic in naturally sown grasslands where environmental factors, namely flood, largely influence vegetation. This approach requires more resources for image acquisition, fieldwork, and botanical expertise than topographical approaches. However, these constraints are balanced by deeper insight into habitat selection of species, even in homogeneous landscapes, and probably the providing of more robust information to base on to delineate areas for conservation.

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575

SUPPLEMENTARY MATERIAL

Table S1. Model selection for mapping the ewetness index using the MuMin R package. Only models with ΔAICc <1.5 are shown. Description of variables are given in Table 1 (1-1_ refer to ID index.

Intercept	Coefficient estimates																		Df	logLik	AICc	ΔAICc	Weight
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18					
114.10	0.19			49.73			1.65	-164.96							-0.65				7	-110.97	237.08	0.00	0.00048
115.33				49.95		0.19	1.48	-167.03							-0.66				7	-111.02	237.18	0.10	0.00046
105.32				42.22			1.36	-155.15		0.17					-0.59				7	-111.13	237.40	0.32	0.00041
107.07		0.17		44.44			1.55	-156.43							-0.55				7	-111.17	237.47	0.39	0.00040
84.54		-1.12		25.56				-131.68		1.25					-0.77				7	-111.36	237.85	0.77	0.00033
60.41	3.29	-6.90						-109.44		3.71		-2.71			-1.48				8	-110.40	238.27	1.19	0.00027
78.70		-1.57				1.67		-159.23			45.54				-0.93				7	-111.67	238.48	1.40	0.00024
-19.01	5.30	-8.37								2.98		-2.36			-1.57	3.85			8	-110.52	238.51	1.44	0.00023
139.51	1.12	-0.96	-56.04				1.70	-185.53							-0.86				8	-110.53	238.52	1.45	0.00023
139.25	1.11	-0.95					1.70	-185.38	-37.46						-0.86				8	-110.53	238.53	1.45	0.00023
139.19	1.11	-0.95			-56.21		1.70	-185.35							-0.86				8	-110.53	238.53	1.45	0.00023
100.51	0.10				-32.83		1.29	-142.17							-0.43				7	-111.71	238.54	1.47	0.00023
100.49	0.10						1.29	-142.13	-21.86						-0.43				7	-111.71	238.55	1.47	0.00023

100.38	0.10	-32.55	1.29	-141.93	-0.43	7	-111.72	238.56	1.49	0.00023	

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